

NEW GENERA OF LOWER CARBONIFEROUS SPIRIFERID
BRACHIOPODS (BRACHIOPODA: SPIRIFERIDA)

JOHN L. CARTER

Curator, Section of Invertebrate Paleontology

ABSTRACT

Two new genera of imbricate North American spiriferoid brachiopods are *Tegulocrea*, type species *Spirifer incertus* Hall 1858, and *Fernglenia*, type species *Spirifer vernonensis* Swallow 1860, assigned to the new family Imbrexiidae.

A group of closely related and morphologically similar North American species of the genus *Spirifer* are differentiated from the type species of the latter on the basis of their distinctive growth form. *Mesochorispira* is proposed as a new subgenus of *Spirifer* Sowerby, 1816, with *Spirifer grimesi* Hall 1858, as the type species.

INTRODUCTION

In connection with compiling and revising the families and genera of the Late Paleozoic and Mesozoic spiriferid brachiopods for the proposed new edition of the Treatise on Invertebrate Paleontology, it became apparent that several species of North American Lower Carboniferous spiriferids could not be placed in any existing spiriferoid genus. Three groups of such species can be distinguished clearly and are described as new genera or subgenera herein.

Two of the new genera delineated here are assigned to a new family, the Imbrexiidae, which is characterized by having imbricate ornament and moderately to freely bifurcating strong ribs on the lateral slopes and fold-sulcus. The systematic position of this family is discussed below.

A closely related group of several species of the cosmopolitan Lower Carboniferous genus *Spirifer* Sowerby, 1816, constitutes a morphologically distinctive lineage. These species are segregated from *Spirifer striatus* and are described as a new subgenus.

SYSTEMATIC PALEONTOLOGY

The specimens illustrated in this paper are deposited in the collections of the Section of Invertebrate Paleontology, The Carnegie Museum of Natural History.

Superfamily Spiriferoidea King, 1846

[*nom. correct.* Carter, herein (*pro* superfamily Spiriferacea King, 1846, *nom. transl.* Schuchert, 1896, p. 333, *ex* Spiriferidae King, 1846, p. 28)]

Family Imbrexiidae, new family

Diagnosis.—Entirely costate, subquadrate spiriferoideans with width of hinge-line equal to or slightly greater than maximum width; fold and sulcus well developed, medially subangular, flaring in some genera; ventral interior with short to moderately long dental adminicula and short delthyrial plate; ornament con-

sisting of moderately numerous strong simple or bifurcating costae; micro-ornament consisting of weak capillae and regularly imbricate growth lamellae.

Genera assigned.—*Imbrexia* Nalivkin 1937, *Fernglenia* n. gen., *Tegulocrea* n. gen., ?*Ala* Nalivkin, 1979.

Stratigraphic range.—?Middle Tournaisian; Upper Tournaisian or early Osaegan.

Remarks.—This family is readily differentiated from most of the other spiriferoid families by its imbricate growth lamellae. Some genera of the Neospiriferidae are weakly to moderately imbricate but the tegulate lamellae are usually confined to the anterior portion of the shell. Imbresiids, in having well-developed imbricate lamellae on the entire surface of the shell, are similar to members of the superfamily Paeckelmanelloidea. The imbresiids differ from the paeckelmannelloids in having a subquadrate outline and more numerous ribs that commonly bifurcate over the entire surface. Paeckelmannelloids have fewer simple costae on the flanks and the sulcus is usually smooth or with a single rib. In addition, they usually have a widely subtrigonal outline and the Late Devonian and Lower Carboniferous genera are usually much smaller than imbresiids.

Carter (1974:684) assigned *Imbrexia* Nalivkin to the subfamily Spiriferinae on the basis of its spreading fold-sulcus and bifurcating costae. No other member of the subfamily Spiriferinae possesses an imbricate ornament. The description of two additional imbricate genera which share several diagnostic morphological characters with *Imbrexia* implies a natural grouping. For these reasons these genera are separated from the Spiriferidae into a new family.

The relationship of the members of this new family to the other taxa within the superfamily Spiriferoidea is not obvious. Two of these genera appear cryptogenically at nearly the same level in the lower Burlington Limestone (Upper Tournaisian) or equivalent strata in central North America. *Fernglenia* n. gen., based on *Spirifer vernonensis* Swallow, seems to have appeared slightly before *Imbrexia* Nalivkin or *Tegulocrea* n. gen., possibly in the late Middle Tournaisian. If that is true, then the small number of bifurcating costae in this genus may be significant and may represent the most primitive condition of the ornamentation in this group, a very important character in spiriferoid phylogeny and classification.

Ala Nalivkin also appeared at this approximate horizon in the Upper Tournaisian of the Ural Mountains. Nalivkin (1979) compared his new genus to *Podtshermia* Kalashnikov 1966, although it is much more similar externally to the genus *Imbrexia*. I recently examined the holotype of *Ala* and could not detect micro-ornament or imbricate growth lamellae due to incomplete preservation of the primary shell layer. Whether or not *Ala* is imbricate cannot be determined at present. If it proves to be imbricate, its affinities lie with this new family. If not, Nalivkin probably was correct in aligning it with *Podtshermia* Kalashnikov 1966. Externally it is very similar to *Imbrexia* except for occasional trifurcations of the primary umbonal ribs.

A moderate number of mostly simple ribs in *Fernglenia* n. gen. suggests derivation from some member of the subfamily Prospirinae Carter 1974. For example, some species of *Prospira* Maxwell and *Unispirifer* Campbell are strongly imbricate anteriorly but have smooth non-imbricate posterior valves. The development of imbricate growth lamellae much earlier in ontogeny of a similar species would result in the completely imbricate ornament seen in the imbresiids. Bifurcating costae on the lateral slopes of the prospirins are rare as in the (undescribed) earliest

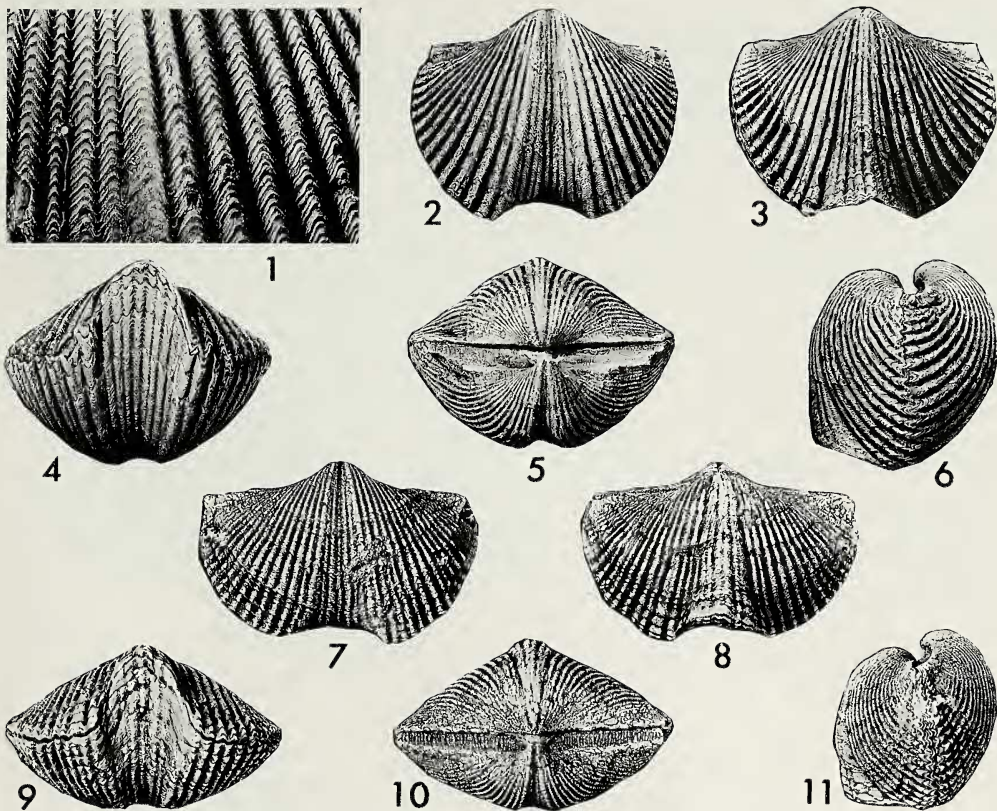


Fig. 1.—*Fernglenia vernonensis* (Swallow). 1.1, imbricate micro-ornament, near mid-valve of an adult specimen from the Nunn Member of the Lake Valley Formation at Apache Hill, Sierra County, New Mexico (SL626), CM 35002, $\times 4$; 1.2–1.6, ventral, dorsal, anterior, posterior, and lateral views of a medium-sized rotund specimen from the Fern Glen Formation at Glen Park Station (abandoned), Jefferson County, Missouri (SL1037), CM 35003, $\times 1$; 1.7–1.11, ventral, dorsal, anterior, posterior, and lateral views of a complete but partially and coarsely silicified, medium-sized specimen from the Fern Glen Formation at Fern Glen Station, St. Louis County, Missouri (SL1038), CM 35004, $\times 1$.

species of *Fernglenia* from the Caballero Formation of New Mexico, another prospirin character.

***Fernglenia*, new genus**
(Fig. 1.1–1.11, 2)

Type species.—*Spirifer vernonensis* Swallow 1860, p. 644.

Etymology.—Named for the now defunct Fern Glen Station, St. Louis County, Missouri.

Other species assigned.—Besides the type species there are two undescribed species in North America. One is a smaller more globose species with rare bifurcations, from the Caballero Formation of New Mexico. It has a narrower and more weakly developed fold and sulcus than *F. vernonensis* and is found in slightly older strata. The other undescribed species occurs in the Banff Formation of Alberta. It differs from the type species mainly in having more numerous bifurcations on the lateral slopes. Neither of my collections of these species is adequate for description and illustration.

Diagnosis.—Medium-size imbrexiids with moderately coarse mostly simple costae on lateral slopes; outline transversely subquadrate to subelliptical; cardinal

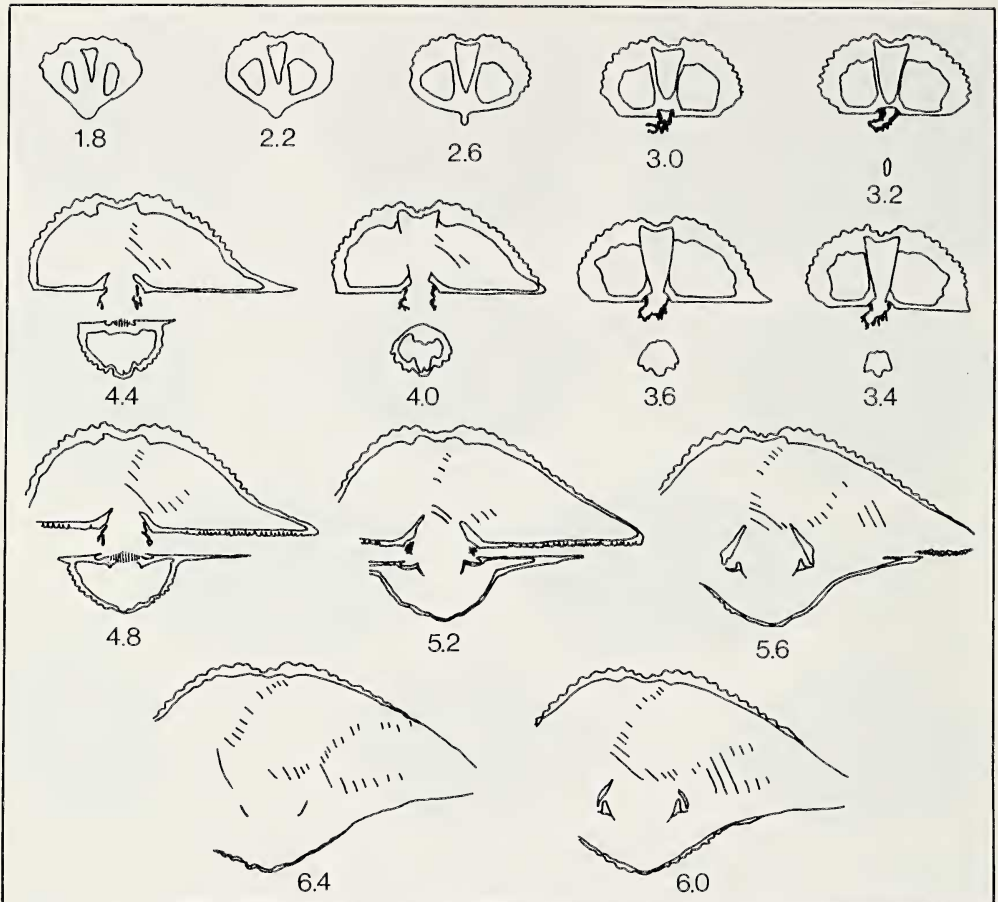


Fig. 2.—Transverse serial sections of a medium-sized specimen of *Fernglenia vernonensis* (Swallow) from the Nunn Member of the Lake Valley Formation at Apache Hill, Sierra County, New Mexico (SL626), CM 35005, $\times 1.5$. Numbers refer to distance in millimeters from ventral beak.

extremities mucronate in juveniles, truncated or slightly mucronate in adults, rarely alate; maximum width attained at hingeline or anteriorly near mid-length; both valves well inflated but dorsal valve not as convex as ventral; fold and sulcus well defined, usually with seven or more costae and a simple median sulcal costa; first lateral costa bounding fold invariably bifurcates; dental adminicula moderately long for family.

Comparisons.—The strong usually simple costae and well-inflated profile of this genus serve to differentiate it from other genera in this family. *Imbrexia* Nalivkin is usually larger with binary costae on the lateral slopes and an anteriorly flaring fold and sulcus. *Tegulocrea* n. gen. has a less inflated profile and much finer more freely bifurcating ribs on the lateral slopes. *Ala* Nalivkin, if it belongs here, is much larger with more numerous freely bifurcating or even trifurcating ribs on the lateral slopes.

Remarks.—The type specimens of the type species of this new genus were destroyed in a fire in the late 19th century at the University of Missouri. A neotype has not been chosen. To further complicate matters Swallow (1860:644) did not

illustrate his new species nor did he provide a type locality, referring it only to the "Chemung" of St. Louis County, Missouri. Weller (1909) was the first to illustrate and redescribe this species, correctly interpreting Swallow's reference to the "Chemung" as being the same horizon as his Fern Glen Formation. Weller originally regarded the Fern Glen to be of Kinderhookian age (which 19th century workers referred to as "Chemung") but later (1926:325) reassigned it to the Osagean. Weller (1909:303) asserted that "Swallow's type specimens of this species were collected at the locality now known as Fern Glen." How he came to this knowledge is not stated, but it is possible that he saw Swallow's type collection at the University of Missouri before it was destroyed.

If we accept Weller's statement as fact, then the Fern Glen exposed in the railroad cut near Fern Glen Station, St. Louis County, Missouri, is the type locality for this species. The Fern Glen Formation itself was first described by Weller from the exposures at Glen Park Station, Jefferson County, Missouri. In Fig. 1, nearly complete specimens are illustrated from each of these localities. The specimen from Fern Glen Station (Fig. 1.7-1.11) is partially silicified and indifferently preserved but is otherwise characteristic of this species in both size and outline. The Glen Park Station specimen (Fig. 1.2-1.6) is well preserved but is unusually rotund for this species. Fig. 2 shows transverse serial sections of the interior of *F. vernonensis* from the Nunn Member of the Lake Valley Formation, New Mexico.

Stratigraphic range.—?Late Kinderhookian, Early Osagean (?M. Tournaisian, U. Tournaisian).

***Tegulocrea*, new genus**
(Fig. 3.1-3.34, 4)

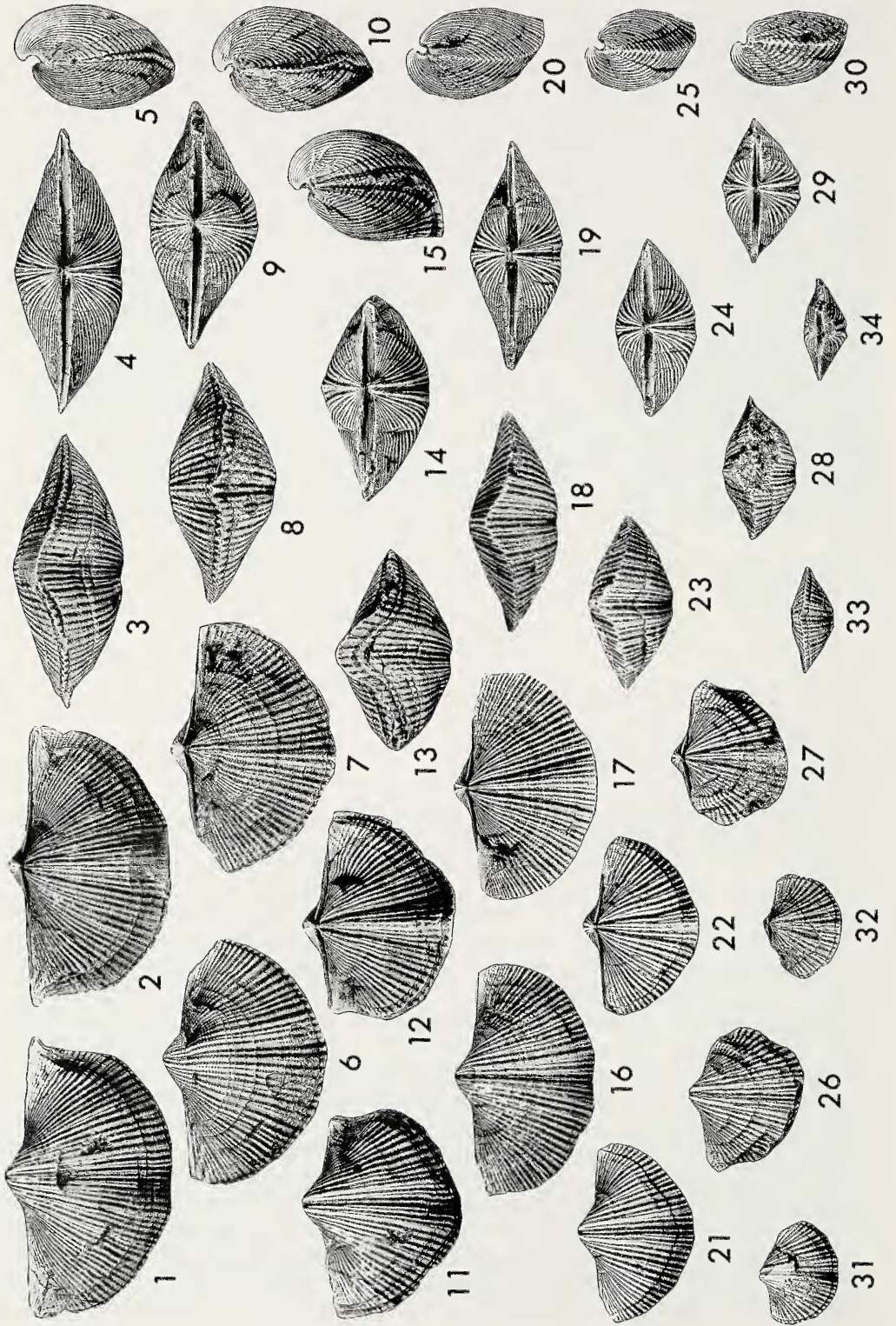
Type species.—*Spirifer incertus* Hall 1858, p. 602.

Etymology.—*tegula* (L.), tile; *ocrea* (L.), sheath or husk.

Other species assigned.—*Spirifer tenuicostatus* Hall 1858, *Spirifer tenuimarginatus* Hall 1858. According to Weller (1914:356), the latter species may be a synonym of the former.

Diagnosis.—Slightly smaller than average imbrexiids; outline subquadrate to subsemicircular; profile lenticular, only moderately inflated; both valves moderately convex, dorsal usually slightly less convex than ventral, often flattened or weakly concave near lateral extremities; cardinal extremities subangular to slightly mucronate in adults, slightly rounded in juveniles; maximum width usually attained at or near hingeline; fold and sulcus moderately developed, moderately narrow to broad, flaring anteriorly to incorporate additional costae from lateral slopes in large adults; sulcus often poorly delineated from lateral slopes with rounded borders; fold well defined anteriorly, sometimes subcarinate; entire surface with numerous fine imbricate costae some of which bifurcate or, more rarely, trifurcate freely; costae in sulcus moderately numerous, median costa simple, lateral ones often bifurcating; first lateral costa bounding fold invariably bifurcating in umbonal region; dental adminicula short or rudimentary.

Comparisons.—This new genus can be differentiated from other members of this family by its modest size, thinner profile, finer ribbing and very short or rudimentary dental adminicula. It is similar to *Ala* Nalivkin in its freely bifurcating or even trifurcating ribbing but the costae are finer. The cardinal extremities of *Ala* appear to be rounded in all growth stages, not mucronate or angular as in adults of *Tegulocrea*. As discussed above, it is not known whether or not *Ala* is imbricate.



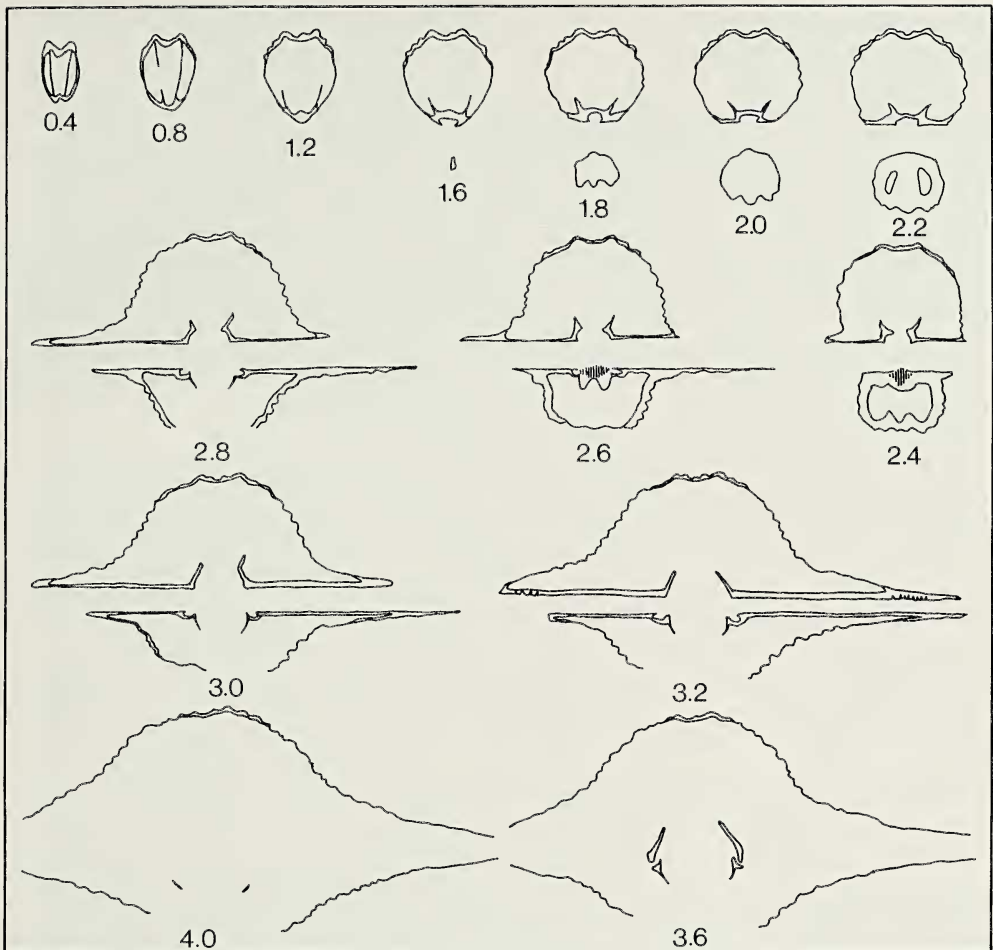


Fig. 4.—Transverse serial sections of a medium-sized specimen of *Tegulocrea incerta* (Hall) from locality SL407, CM 35013, $\times 2.5$. Numbers refer to distance in millimeters from the ventral beak.

Remarks.—The type of *Spirifer incertus* Hall, from the Burlington Limestone at Burlington, Iowa, is in the collections of the American Museum of Natural History. It is a crushed incomplete specimen. Weller (1914:pl. 51) illustrated this holotype plus a fine large complete shell and an excellent ventral valve, both also from the Burlington Limestone at Burlington. This species is rare in the Burlington Limestone and has not been cited in the North American literature since Weller (1914).

The growth series illustrated herein (Fig. 3) is from a small bioherm in the St. Joe Formation at Kenwood, Mayes County, Oklahoma. This fauna is judged to be of lower Burlington age. The collection includes several large incomplete specimens comparable in size to Weller's large specimens but most of the specimens

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Fig. 3.—*Tegulocrea incerta* (Hall). 3.1–3.34, ventral, dorsal, anterior, posterior, and lateral (no lateral view for the small specimen) views of a growth series of seven nearly complete specimens from the St. Joe Limestone near Kenwood, Mayes County, Oklahoma (SL407), CM 35006–35012, $\times 1$.

fall within the size range seen on Fig. 3. Internal details can be seen in Fig. 4, a series of tranverse sections.

Stratigraphic range.—Osagean (Upper Tournaisian–Middle Visean).

Family Spiriferidae King, 1846
Subfamily Spiriferinae King, 1846

Genus *Spirifer* Sowerby, 1816

This cosmopolitan genus has been identified in many brachiopod faunas of Lower Carboniferous age. Recognition of the true affinities of the type species, *Spirifer striatus* (Martin, 1793) has progressed slowly over the past century or so.

In the first edition of the brachiopod volumes (Part H) of the Treatise on Invertebrate Paleontology (Pitrat, 1965), the genus *Spirifer* was still grouped with morphologically diverse genera. I have assigned those genera to four different families in two superfamilies for the next edition of the Treatise.

In 1974, I restricted the subfamily Spiriferinae to genera with numerous bifurcating costae on the entire valve surfaces and with a poorly delimited fold-sulcus. As thus constituted it included the following genera: *Spirifer* Sowerby 1816, *Imbrexia* Nalivkin 1937, *Grandispirifer* Yang 1959, *Podtsheremia* Kalashnikov 1966, and *Warsawia* Carter 1974. Poletaev (1986) removed *Podtsheremia* and assigned it to his new subfamily Pudonellinae that is characterized by having a consistently narrow hingeline with rounded cardinal extremities in all growth stages.

As seen above, I have further restricted the Spiriferinae by removal of the genus *Imbrexia* Nalivkin to a new family, the Imbrexiidae. Therefore, as presently defined, the Spiriferinae include only transverse genera with numerous bifurcating costae on the entire valve surfaces and a poorly delimited fold and sulcus.

Of course, this reexamination of the spiriferid genera prompted a reexamination of the concept of the genus *Spirifer* itself. Unfortunately, a review of all the Carboniferous species assigned to this widely identified genus is far beyond my resources. There are few collections of Eurasian species of *Spirifer* sensu stricto in the United States. However, it has been possible to reexamine the North American species assigned to this genus as it is now defined. The result of this study convinces me that four or more North American species are closely related, forming a lineage that ranges in age from late Kinderhookian to late Osagean (Middle Tournaisian–Middle Visean). These species are consistently and readily differentiated from the type species, *Spirifer striatus*, on purely morphological grounds which justifies separation as a subgenus. Separating these North American species from *Spirifer striatus* and its close allies at the genus level may not be tenable on the basis of growth form alone. The consistency of growth form in the type species and its closely related congeners is not readily ascertainable from the literature. I suggest that they seem to be characterized by having a moderately to strongly transverse alate to mucronate growth form in all but the earliest growth stages which presumably are rounded. I have not observed this latter detail but infer that a wide acute hingeline is unlikely to occur in brachiopod spat.

Spirifer (*Spirifer*) Sowerby, 1816

Type species.—*Conchylolithus* (*Anomia*) *striatus* Martin, 1793, pl. 23.

Other species assigned.—*Spirifer baiani* Nalivkin 1937, *Spirifer ischimicus* Litvinovitch 1962, *Neospirifer karagai* Litvinovitch 1962, *Spirifer cascadenis* Warren 1927, ?*Spirifer mountraensis* Carter 1987.

Diagnosis.—Medium to large, transverse; outline subtrigonal to subsemicircular; cardinal extremities alate, mucronate or angular in all observable growth stages.

Remarks.—The earliest species of this subgenus known to me is *Spirifer cascadenis* Warren from the middle Banff Formation of Alberta, Canada. Its age is judged to be very late Kinderhookian or late Middle Tournaisian, slightly younger than the first occurrence of *Spirifer (Mesochorospira) gregeri* Weller which is from the preceding faunal unit of Carter (1991). The antecedents of *Spirifer cascadenis* are not known. Its appearance is cryptogenic. *Spirifer mountraensis* Carter 1987 is queried because in large adults it has angular truncated cardinal extremities. In earlier growth stages it is alate and strongly transverse.

Stratigraphic range.—Late Middle Tournaisian–Lower Namurian.

***Spirifer (Mesochorospira)*, new subgenus**

Fig. 5, 6

Type species.—*Spirifer grimesi* Hall 1858, p. 604 (the two syntypes in the University of Illinois collections are from the Burlington Limestone at Burlington, Iowa). This species is widely distributed in Early Osagean (Upper Tournaisian) rocks throughout the mid-continent and the southern Cordilleran region.

Etymology.—*mesos* (Gr.), middle; *choros* (Gr.), land or country; *spira* (Gr.), spire. The name refers to the geographic distribution of this taxon in the North American mid-continent.

Other species assigned.—In addition to the type species the following taxa are placed here: *Spirifer gregeri* Weller 1914, *Spirifer rowleyi* Weller 1909, and *Spirifer logani* Hall 1858. *Spirifer striatiformis* Meek 1875 may be assigned here although it is significantly smaller than the foregoing species. *Spirifer esplanadensis* Brown 1952 is small and has an unusual low fold in the bottom of the sulcus but otherwise is similar to the above species.

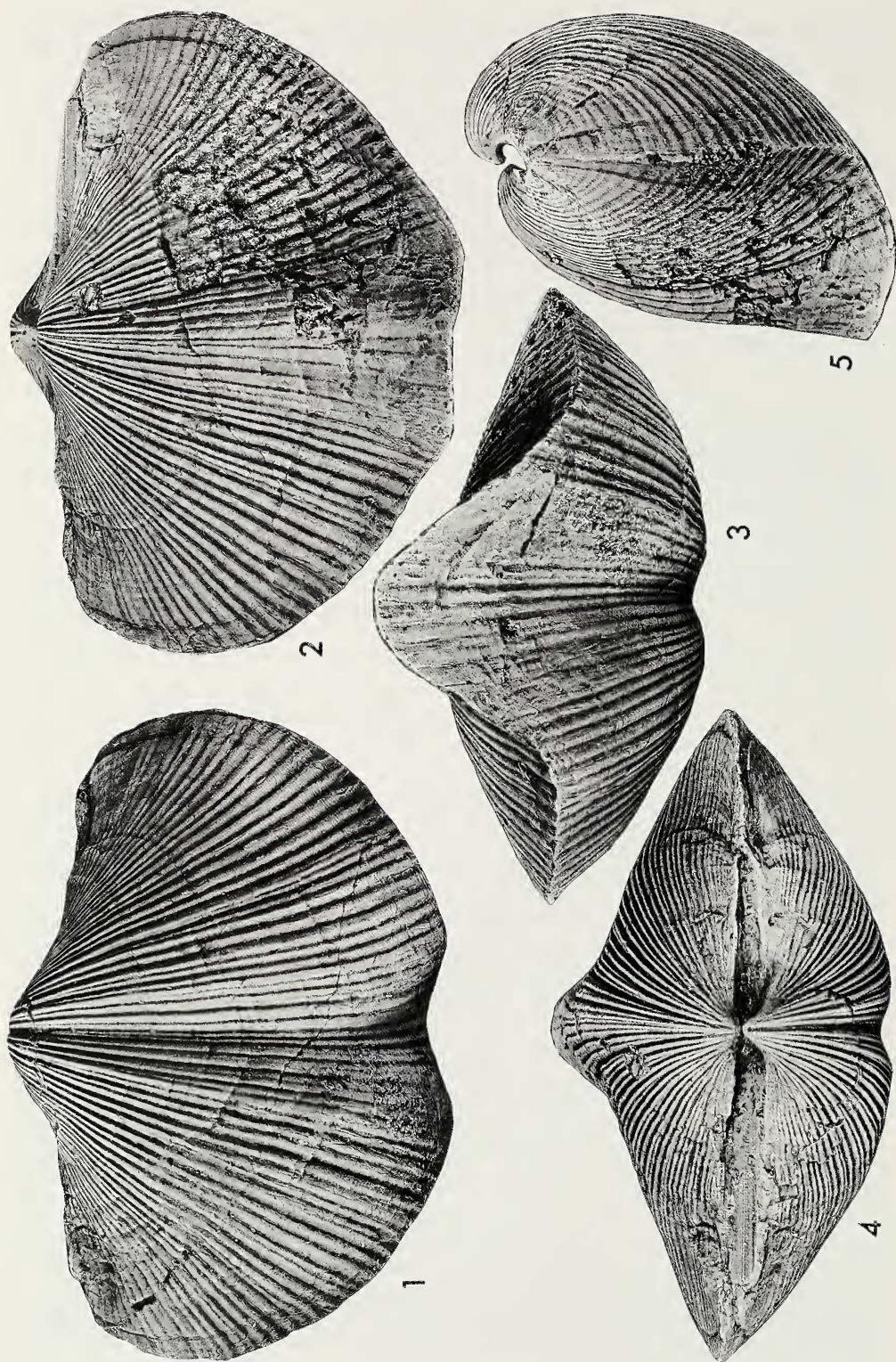
Other possible members of this subgenus occur in Belgium and Russia. The Belgian Upper Tournaisian species Koninck (1887) incorrectly referred to *Spirifer cinctus* Keyserling 1846 (plate 24, fig. 6, 7; plate 26, fig. 1–4) and *Spirifer subcinctus* Koninck 1883 (plate 24, fig. 4, 5; plate 26, fig. 9–11) are of similar size and posterior growth form to *Spirifer grimesi*, as is *Spirifer subgrandis* Beznosova 1959 from the Upper Tournaisian of the Kuznets Basin.

Diagnosis.—Medium-sized to large *Spirifer* with transverse to elongate subovate outline; with double reversal in growth form, from rounded cardinal extremities in juveniles, to slightly transverse mucronate cardinal extremities at mid-size, and back to rounded cardinal extremities in adults.

Remarks.—Weller's (1914:361) description of the type species is still applicable as are his comparisons with similar species. Fig. 5 shows a large transverse, well-preserved, nearly complete individual of the type species from the St. Joe Formation of Oklahoma that illustrates well the ornamentation and rounded cardinal extremities. In Fig. 6 posterior views of two incomplete specimens from the Burlington Limestone of Missouri show the growth lines that indicate a double reversal of growth form during ontogeny.

The closeknit group of species from the upper Mississippi Valley region consisting of *Spirifer gregeri* from the upper Chouteau and Sedalia Dolomite, *Spirifer rowleyi* from the Fern Glen Formation, *Spirifer grimesi* from the Burlington Limestone, and *Spirifer logani* from the Keokuk Limestone clearly form a lineage. The immediate progenitor of the earliest species, *Spirifer gregeri*, is not known. This species first occurs in the Late Kinderhookian (Middle Tournaisian) Chouteau Limestone of northeastern Missouri and is possibly the earliest known occurrence of the genus *Spirifer* or the subfamily Spiriferinae.

A possible, or even likely, generic ancestor for this group is the Late Famennian–Early Kinderhookian prospirin genus *Paralellora* Carter 1974, which also occurs



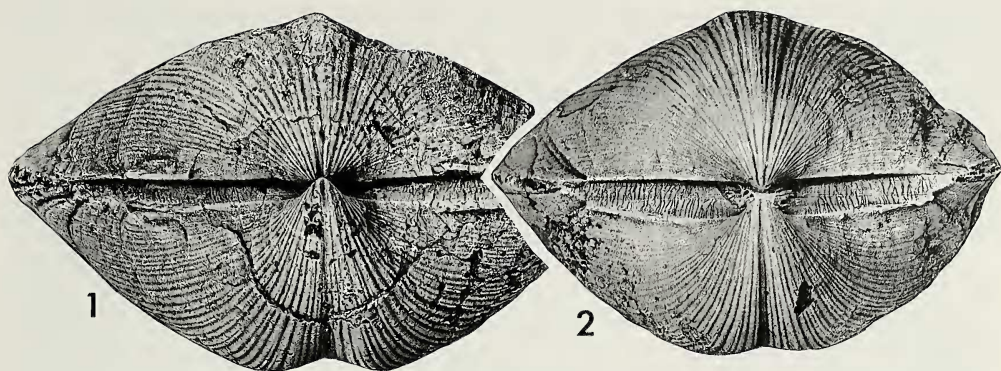


Fig. 6.—*Spirifer (Mesochorispira) grimesi* Hall. 1, 2, posterior views of two specimens from the lower Burlington Limestone at Louisiana, Missouri (SL854) showing ontogenetic changes in growth form as indicated by the growth lines, CM 35015, 35016, $\times 1$.

in the upper Mississippi Valley region. This genus is of medium size and is characterized by having moderately numerous costae that bifurcate freely in large adult specimens of the youngest known species, the early Kinderhookian *P. nupera* Carter 1988. The growth form of this species is similar to that of *Mesochorispira*, that is to say, rounded in the very earliest stages, transversely mucronate in middle growth stages, and becoming rounded again in adults. *Paralellora* is assigned to the subfamily Prospirinae on the basis of its modest number of costae on, and clear delineation of, the fold-sulcus. The stratigraphic interval between the last occurrence of *Paralellora* and the first appearance of *Spirifer (Mesochorispira)* is currently devoid of similar spiriferids in North America.

Stratigraphic range.—Late Kinderhookian–Late Osagean (Middle Tournaisian–Middle Viséan).

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Fig. 5.—*Spirifer (Mesochorispira) grimesi* Hall. 5.1–5.5, ventral, dorsal, anterior, posterior and lateral views of a nearly complete large transverse specimen from the St. Joe Limestone at the same locality (SL407) as the specimens in Fig. 3, CM 35014, $\times 1$.

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